

CLARK (T. Earl) Compliments of
Tracy Clark
Pembroke, W. Y.

Comparative Anatomy of the Insula.

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BY

TRACY EARL CLARK, B.S.

With Five Plates.

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THE COMPARATIVE ANATOMY OF THE INSULA.

TRACY EARL CLARK, B.S.

With Plates IX-XIII.

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The importance attached to this region of the human brain and the wide divergence of opinion as to the existence of an homologous area in other mammals led the writer, at the suggestion of Professor Burt G. Wilder, to select it in 1890 as the subject for his baccalaureate thesis. The extensive neurologic literature and abundant material possessed by the Anatomical Department of the Cornell University soon convinced the writer of his inability to cover more than the macroscopic side of the subject and that upon a very few specimens. Later the kind offer of Professor Wilder to place at his disposal all of the material at hand led to the prosecution of the work somewhat further.



It is with a keen sense of gratitude that I now acknowledge my indebtedness to Professor Wilder whose advice has been frequently sought and who has always shown great interest in the work. I desire also to thank Professor Simon H. Gage and Instructor Pierre A. Fish for their interest and assistance, and Mrs. S. P. Gage for the loan of specimens.

The following list, while incomplete, will give some idea of the extent and nature of the material upon which the writer has based his conclusions. The accession numbers are the serial numbers in the Accession Book of the Department of Vertebrate Zoology of the Cornell University.

Ac'n No.	Sex.	Age.	Groups.
			SUB-CLASS I. PROTOTHERIA.
			ORDER I. MONOTREMATA.
76	Male		<i>Ornithorhynchus anatinus</i> , duck-bill.
			SUB-CLASS II. METATHERIA.
			ORDER II. MARSUPIALIA.
			<i>Didelphys virginiana</i> , common opossum.
			Several specimens.
378			<i>Macropus giganteus</i> , giant kangaroo.
			Two specimens.
1331	Male	}	<i>Hypsiprymnus moschatus</i> , kangaroo-rat.
108	Male		
			SUB-CLASS III. EUTHERIA.
			ORDER III. EDENTATA.
			No specimens.
			ORDER IV. SIRENIA.
844	Male	Adult	<i>Manatus americanus</i> , American manatee.
			ORDER V. CETACEA.
670	Male	Adult	<i>Globiocephalus melas</i> , pilot-whale, black-fish. Fig. 35.
			ORDER VI. UNGULATA.
2177	Male		<i>Camelus bactrianus</i> , Bactrian camel.
2122	Male		<i>Camelus dromedarius</i> dromedary. Fig. 22.
776			<i>Cariacus clama</i> , fallow deer.
961	Male		<i>Cariacus virginiana</i> , Virginia deer, red deer. Fig. 23.
			<i>Ovis aries</i> , domestic sheep. Figs. 32-34.
			Many specimens.
3408	Female	Adult	<i>Bos taurus</i> , domestic cow. Figs. 26-30.
3409	Female	Adult	
3362	Female	Juv.	
		Juv.	
2777			<i>Equus caballus</i> , domestic horse.
2840		6 mo.	" " " "
2123	Male	Term	" " " "
2095	Male	Adult	" " " "
2259	Male	Juv.	<i>Equus asinus</i> , burro. Fig. 24.
			Fig. 25.

Ac'n No.	Sex.	Age.	Groups.
			ORDER VI. UNGULATA—Continued.
			<i>Sus scrofa</i> , domestic pig.
			Many specimens.
2123			<i>Tapirus malayanus</i> , Malayan tapir. Fig. 31.
			ORDER VII. TOXODONTIA.
			Fossil.
			ORDER VIII. HYRACOIDEA.
			No specimen.
			ORDER IX. RODENTIA.
			<i>Arctomys monax</i> , woodchuck, marmot.
			<i>Castor fiber</i> , beaver.
			<i>Lepus cuniculus</i> , rabbit.
			Several specimens.
			<i>Mus decumanus</i> , brown rat.
			<i>Mus musculus</i> , common mouse.
			<i>Sciurus hudsonius</i> , red squirrel.
			ORDER X. PROBOSCIDA.
2181	Female		<i>Elephas indicus</i> , Indian elephant. Fig. 21.
166			ORDER XI. CARNIVORA.
3124		5-8 wk }	<i>Canis familiaris</i> , domestic dog. Figs. 14-18.
			Many specimens.
277	Male		<i>Lynx rufus</i> , American wild-cat, lynx.
157	Female	22 da.	<i>Felis leo</i> , African lion.
309	Female	18 yrs.	<i>Felis concolor</i> , puma, panther. Fig. 10.
			<i>Felis pardalis</i> , ocelot.
			<i>Felis domestica</i> , domestic cat. Fig. 19.
			Many specimens.
			<i>Hyaena striata</i> , hyaena.
2031	Male		<i>Procyon lotor</i> , raccoon. Figs. 11 and 12.
			Several other specimens.
			<i>Mephitis mephitis</i> , skunk. Fig. 20.
			Several specimens.
			<i>Putorius vison</i> , mink.
197			<i>Putorius domestica</i> , ferret.
			<i>Phoca vitulina</i> , seal. Fig. 9.
a645	Male	Juv.	<i>Ursus thibetianus</i> , Thibet-bear. Fig. 13.
			ORDER XII. INSECTIVORA.
3356			<i>Condylura cristata</i> , star-nose mole.
			<i>Sorex platyrhinus</i> , common shrew, shrew mouse.
			ORDER XIII. CHEIROPTERA.
			<i>Vespertilio subulatus</i> , common brown bat.
			Several specimens.
			ORDER XIV. PRIMATES.
265	Female	Juv.	<i>Anthropopithecus troglodytes</i> , Chimpanzee. Fig. 7.
			<i>Cercopithecus fuliginosus</i> .
			<i>Macacus</i> . Fig. 8.
			Several specimens.
			Numerous preparations of the human brain at various ages. See Figs. 1-6.

HISTORICAL SKETCH.

Vicq d' Azyr (16, 1786) seems to have been the first to call attention to this area in the human brain. He refers (Pt. II, p. 26) to it as "the convolutions situated between the Sylvian fissure and the corpus striatum" and again (Pt. II, p. 74) as "the convolutions which accompany the Sylvian fissure." These references would seem to indicate that at that time all that was known was the fact of the existence of certain gyres in that region which, on account of their concealed position, had attracted but little attention; furthermore these are the only references made to this region in his volume of several hundred pages.

Monro (42, 1788) pictured three gyres of the human insula seen after the removal of the ventral portion of the cerebrum, but he neither named nor described them.

Hence it remained for Joh. Christ. Reil (1804-1806) to give the first description as follows: "Die Insel hat eine länglichrunde Gestalt." Since that time the area has been known as the "insula" or "island of Reil," although many other names have from time to time been applied to it (see Synonymy, p. 93.)

The insula seems to have attracted little attention during the next half century and it was not until about 1860 that the study of cerebral localization caused increased importance to be attached to it. Until several years later it was supposed that the insula governed, at least in part, the power of articulate speech. Authors had noted that in aphasics there was generally a lesion of the insula and the left subfrontal gyre. They seem not, however, to have taken account of lesions confined strictly to either area and they assumed that the insula had been first affected and that later the lesion had extended into the adjoining area. Broca (4) disproved this. By comparing the lesions found in postmortems upon a large number of aphasic patients he reached the conclusion as early as 1861 that the faculty of speech was located in the left subfrontal gyre, still often called "Broca's convolution." During the next seven

years a large number of aphasics were examined for the purpose of verification, and in 1868 he published a résumé of the facts upon which he based his conclusion. This discovery naturally aroused great interest in the insula inasmuch as "lesions of the left subfrontal gyre generally extend into the insula," while those (2) "confined strictly to the insula are very rare." In 1868 Broca (4, 113) pointed out that in aphasics there is almost always a lesion in the caudal half of the subfrontal gyre of either the right or the left side, and that this lesion is sometimes confined exclusively to this area. However, in about one case in twenty this area is apparently perfectly sound, but a lesion exists in the insula or an adjacent gyre with which the subfrontal is continuous. The lesion is located in about 19 out of 20 times on the left side and the right side remains perfectly sound. He had never found a case in which the patient was possessed of this faculty and at the autopsy showed a lesion of both subfrontal gyres. Speech has, however, persisted in some patients where an autopsy showed the total destruction of the right subfrontal. He also said he had noticed several cases of idiots who had never been able to learn to read, where the subfrontal gyre was absent on both sides.

So far as the writer has been able to learn, no satisfactory reason has ever been given for this strange association of the subfrontal region and the insula; yet if, as Meynert (38) says, "fibers from the subfrontal gyre pass just entad of the insular cortex," then it would seem very likely that a diseased condition of those fibers sufficient to cause loss of speech would affect the overlying cortex of the insula producing lesions and perhaps a breaking down of the cellular cortex, as frequently happens. A clot of blood, through pressure upon the insula, has also been said to cause loss of speech.

THE DEVELOPMENT OF THE OPERCULUMS.

In 1892, Cunningham (15, 78) said of the human brain: "As Mihalkovics has pointed out, it is toward the end of the second month of development that the first signs of the Sylvian depression may be detected. At the same time, it is right to

state that its appearance is frequently delayed beyond this stage and I have observed hemispheres well on in the third month with hardly a trace of it." What is later to become the Sylvian fissure is now only a broad shallow furrow deepest near the base of the brain and radiating in a fan-shape dorsad where it disappears upon the lateral surface. Gradually by the growth of what will later form the frontal, temporal and parietal lobes, an overlapping or folding occurs and the fossa gradually narrows until completely closed. What really happens is that by the more rapid enlargement of these lobes in an enclosed space, the intervening broad area in the bottom of the fossa, which early becomes fixed in position, is finally covered and the lips of the Sylvian fissure are brought together. These overlapping portions are the so-called opercula and in the human brain are four in number, namely: the *operculum* arising from the frontal and parietal, the *preoperculum* and the *suboperculum* from the frontal, and the *postoperculum* from the temporal lobe. These overlapping portions do not differ structurally from the surrounding parts, being convoluted and covered with cinerea on both the ectal and the ental surfaces, and the gyres of the ental surface are interdigitated with those of the insula. The dorso-caudal end of the Sylvian fissure is the part first formed and the first as well to become completely closed. This is due to the rapid growth of the operculum and postoperculum.

In 1890 Beer (1, 309 (ix)) said: "According to Ecker, Mihalkovics, etc., the Sylvian fissure of the adult is formed by the gradual narrowing of a flat broad depression on the lateral surface of the hemisphere, which is due to arrest of development of the *insula Reilii* in the 3rd month of fetal life." The conclusion that the insular area becomes depressed by a cessation of growth, while favored by many neurologists, appears to me unwarranted. Presumably what happens as stated by Wilder is that there is probably no complete arrest of development, but that the surrounding parts develop much more rapidly so that in a short time they project farther laterad, leaving the insula relatively depressed. While this seems to account

for all observed phenomena, the writer is inclined to the belief that one very important factor has been underestimated. During the period when the insula first appears, the brain as a whole is enlarging very rapidly. This enlargement in the region which will later become the Sylvian fissure it is assumed may be due more largely to the expansion of the paracœle than to the thickening of the paracœlian wall by the addition of true nervous substance, which of course is always interstitial. The anatomy of this region would seem to favor this latter conclusion. The intimate connection of the insula with the brain stem is such as to preclude any marked lateral extension and, as the wall of the paracœle is then but little more than membrane, any sudden increase of development, either by addition to the true nervous parietes or by the expansion of the paracœle, would cause the area caudad and dorsad to project laterad giving outline to the insula by the formation of the circuminsular fissure and later the dorsal end of the Sylvian. It also suggests the possibility of finding in a fetus of the fourth to the seventh month an expansion of the paracœle corresponding in a general way to the outline of the rudimentary operculum. The conclusion given above agrees with observations upon the development of this region as described by Cunningham, Ecker and others. It is also further believed that this effect of expansion does not stop here, but that the overlapping of the insula and consequent formation of operculums may be due in part to the expansion of the paracœle, and that the subsequent thickening of the walls by the addition of true nervous substance combined with the effects of growth in an enclosed space may account in part for the continued concealment of the insular area in the adults of Primates and some of the Carnivora.

The exact time of the closing of the Sylvian fissure by the operculums is not known. In 1873, Ecker said it was from the ninth to the tenth month.

In 1888 Mingazzini (41) said: "In one brain of the eighth month, I have found the fissure almost completely closed." The condition here presented I think is one of indi-

vidual difference rather than the rule, as I have examined several brains of this age and have not seen one closed or nearly so.

Broca in 1888 (4, 545) said: "This superficial position of the cephalic extremity of the insula has been observed, more or less, in man, upon a great number of new-born children or those of a few months old; after the second year it is rarely seen except upon the brains of idiots and imbeciles (and also in some deaf-mutes)."

The determination of the exact time of closing of the Sylvian fissure in the normal human brain is of considerable morphologic importance as it marks the completion of a period of remarkable growth of these lobes; and in making a collection of brains between the eighth and twelfth months for this purpose as many as possible should be obtained so that individual differences might not induce a wrong conclusion.

The operculums do not always completely close the Sylvian fissure and hence the insula is exposed sometimes even in the adult human brain. In 1887 Rolleston (49, 35), in his description of an adult male Australian brain, said: "The island of Reil is exposed on the left side. . . The exposure of the island of Reil implies that the surrounding gyri are ill-developed; Broca's convolution is thus shown to be defective, a point of interest in an Australian savage whose language is primitive as shown by its unclassified character." It is questionable if facts would bear out this conclusion, and while some of the gyres might in this specimen have been "ill-developed" it would have been interesting to learn if this had been observed on any other specimen.

The brain of the philosopher Chauncey Wright has a part of the insula exposed. In 1889 Wilder (63, 158) said: "Whether any of this condition is due to pressure during hardening which may have occasioned also the peculiar roundness of the temporal lobe, it is impossible to determine and Dr. Dwight does not recall the condition of the parts when the brain was removed." In others, as that of the Swedish carpenter (No. 318), the operculums not only conceal the insula but abso-

lutely overlap each other. These, with the possible exception of the Australian, are all types of individual difference and their significance may be summed up thus: (1) if the insula is not wholly concealed, it shows that if the insula is normal, the surrounding parts have not reached their full development, while if the insula is abnormally large, the surrounding parts may or may not be fully developed; (2) if the insula is completely covered so that the operculums overlap each other, it would appear that, if the insula is normal, the surrounding gyri must be abnormally developed, while if the insula were unusually small, the normal operculums might even overlap each other.

EARLY DEVELOPMENT OF THE HUMAN INSULA.

We have seen that the rudiments of the Sylvian fissure become apparent toward the end of the second month of fetal life. There is then in the bottom of the shallow fossa an indefinitely-defined oval or somewhat triangular area which apparently develops more slowly than the surrounding lobes and which finally becomes a subarea. As development proceeds, this area becomes more elevated and hence more sharply defined by the formation of the circuminsular fissure. The region thus mapped out is sometimes called the *insular area* because it is the part which will eventually become the insula in man and presents a condition found in the adults of some animals.

Mingazzini (40, 217, 1888) says: "Until the end of the sixth month the insula is quite smooth; constantly there appear in the seventh month those fissures [circuminsular, Wilder; *rigoles*, Broca] which circumscribe the future gyres of the insula. I can therefore not agree with Mikalkovics who asserts that the insula is smooth up to the beginning of the ninth month. I found this quite so once in a brain of the eighth month upon which only one small cortical fissure appeared. In the eighth month, they increase, oftentimes, to the number of four, among which is produced the caudal one which is larger and deeper than the others; after the ninth month, there are, as a rule, four fissures." Mingazzini probably erred in the

above statement. The caudal one of the four fissures on the normal insula is never, so far as the writer has been able to learn, "larger and deeper" than the transinsular fissure which is cephalad of it and the observations of Cunningham (14, 347-348) in 1891 seem to show pretty conclusively that even when three fissures are present on this area, the caudal one is usually in the postinsula.

In the spring of 1890 the writer became convinced, as the result of the study of the comparative anatomy of this region, that future investigation would show that, barring the circuminsular fissure, the transinsular, which is doubtless the most constant and best defined of the fissures on this area, would be found to be the first to appear after the circuminsular and that its homologue exists in some other animals at least. The following table compiled from Cunningham, 1891 (14, 347-348) seems to prove that this really is the order of development in the human fetus. The brains enumerated below range from five to six and a half months.

<i>State of Development of Insula.</i>	CEREBRUMS		Total	Transinsular f. present.
	Right	Left		
Insula perfectly smooth -----	2	4	6	0
" with transinsular fissure -----	3	4	7	7
" " " f. and the one cephalad -----	6	2	8	8
" " " f. one cephalad and one f. caudad -----	2	1	3	3
Totals -----	13	11	24	18

This same author (14, 347) says: " Furthermore, there is good reason to believe that in the development of the sulci and gyri the right insula is usually in advance of the left, and also that the process is greatly retarded in the female brain." The first part of the above statement of Cunningham, while apparently borne out by the table, seems remarkable inasmuch as the left insula in the normal adult is usually larger than the right.

In 1892 Cunningham (15, 15 summary) said: "In the adult brain the insula is proportionately longer in the male than the female. At all periods of growth it would seem that the insula is relatively longer on the left side than on the right side. In

the negro brain, it would appear that the insula is relatively shorter than in the European brain."

The completion of the circuminsular fissure on the ventral side is usually not accomplished until about the time of birth. Prior to this completion of the circuminsular, which is probably influenced to a considerable extent by the cephalic growth of the tip of the temporal lobe, the insula is continuous with the ventral surface of the cerebrum through the Sylvian fossa. It was probably this condition to which in 1885 Meynert (39, 4) called attention as follows: "the island of Reil is connected with a protuberance (the olfactory lobe) situated on the lower aspect of the frontal portion of the fore brain." It will be seen (Figs. 1 and 2) that the lateral root of the olfactory tract extends into the Sylvian fossa (that portion of the Sylvian fissure which does not close up). It is not believed, however, that the fibres of this tract extend over any portion of the insula, but on the contrary that they preserve approximately the same relation to the insula as in the sheep (Fig. 34), the skunk (Fig. 20), the cat (Fig. 19) and the mink, in each of which it is to be noted that the fibres do not pass dorsad of the bottom of the rhinal fissure, thus sharply demarcating the insula from the olfactory lobe.

THE ADULT HUMAN INSULA.

Usually the adult human insula is entirely concealed within the Sylvian fissure and can be seen only by divaricating the lips of the fissure or after cutting them entirely away. Broca (4, 651) says that it is not normally exposed after the second year. This occlusion is a condition found so far as known in all primates and in many of the imprimates. In all brains possessing an insula, the cortex bends in from the lateral surface and passes without interruption under the fissures and over the surface of the insula completely covering it whether convoluted or not. In all brains observed by the writer, the gyres of the operculums are interdigitated with those of the insula.

In 1889 Wilder (63, Prop. CXLI) wrote of this area in man, "the insula is a part of the cortex, which, at one period

wholly superficial, is gradually covered more or less completely by converging folds of the adjacent regions. The insula thus becomes a subgyre, while the operculum, preoperculum, suboperculum and postoperculum are supergyres."

The adult human insula is always sharply demarcated by the surrounding circuminsular fissure (*rigoles*, Broca). Its position is generally in a plane nearly parallel with the lateral surface as shown in Figs. 3 and 4. An exception is shown in Fig 5. In this specimen the gyres form a plane nearly perpendicular to the lateral surface. This is a condition found in the sheep, the pig (12, 9), the calf, and some horses, and is believed to be due to some peculiarity in the development of the brain stem.

In the adult, the insula is a large broad eminence, the surface of which is richly convoluted. It generally possesses from four to six gyres diverging cephalad, dorsad and caudad and producing an appearance not unlike that of a fan. The number of gyres is subject to considerable variation even in the two insulas of the same brain. The brain of Guiteau, the assassin of Garfield, showed marked peculiarities in this respect. According to Spitzka (55, 386) the left insula contained seven fissures and eight gyres, while the right had only five fissures and six gyres. It will be noticed that the right insula had its full complement of fissures and gyres while the left exceeded it by two. Another case markedly different from this one has also been reported by the same author. It, like the preceding, is that of a murderer. He says, the left insula had "fewer and flatter gyri than that [six gyri] of the right side, and was not far different from that of an orang in my possession." In all normal brains, the left insula is said to be larger.

The insula is usually quite deeply fissured and is always divided into two plainly unequal parts. This division is produced by a deep fissure extending dorso-caudad from the ventral side—where it is deepest—to the dorsal margin where it connects again with the circuminsular. This forms a cephalic part, *preinsula*, and a smaller caudal one, *postinsula*. The preinsula is not only larger but contains more gyres. All of the fissures of the insula communicate with the circuminsular dor-

sad but with the exception of the transinsular none of them reach the ventral margin. The area common to all the gyres of the preinsula, and from which they all appear to spring, is usually the part most elevated and is called the *pole of the insula*. Eberstaller (17, 741) says that the "limen insulæ" (pole) is found only or in a certain form in the human brain.

But for the unusually elevated pole in this specimen, Fig. 5 might be said to represent a nearly typical insula. The preinsula usually possesses three gyres of which the first (the one most cephalic) and the third are usually the best developed and these are frequently subdivided dorsad by short fissures. The postinsula seldom possesses more than two gyres the first of which is usually the larger. These gyres are united ventrad and are always longer than those of the preinsula. Eberstaller (17, 741) says the first gyre of the preinsula is the largest and strongest and that the second gyre is usually weakly developed. The postinsulas shown in Figs. 3 and 4 exhibit a peculiarity which is very striking when compared with the usually simple character of the area. The three small elevations of Fig. 3 and the one in Fig. 4 dorsad belong to the postinsula. It is possible that the shallow furrows separating these eminences may have been caused by arterial pressure. Fig. 3 also shows the relation of the insula to the medicornu. The specimen shown in Fig. 5 is remarkable for the unusual elevation of the pole. As previously stated this condition is probably the result of some peculiarity in the development of the brain stem.

In 1887 Waldschmidt (61, 375) said the insula was larger in educated persons. There are many facts favorable to this view but it lacks confirmation.

Eberstaller and Cunningham have each called attention to the apparently intimate relation of the transinsular and central fissures. These fissures are very constant in the human brain, they lie in the same plane, they take the same general direction and they appear in the fetus at about the same time (5-6 mo.). Eberstaller (17, 749, 1887) says: "The cephalic insula is connected wholly with the frontal lobe, the caudal insula with that portion just caudad of the central fissure."

In 1891 Cunningham (14, 338-9) said, that Guldberg had suggested for the transinsular fissure "the very appropriate name of *sulcus centralis insulae* which indicates not only its central position in the island of Reil, but also its relation to the central fissure on the outer surface of the hemisphere mantle." This author then endeavors to establish a connection between gyres and fissures on either side of the transinsular with those on the same side of the central fissure. He further states that "it is true that we cannot regard these corresponding convolutions and sulci as being directly continuous with each other but still in many cases something which approaches very nearly to continuity occurs. Thus it is well known that the inferior precentral sulcus, the fissures of Rolando and the intraparietal sulcus are not infrequently carried downwards, so as to cut into the fronto-parietal operculum and open into the Sylvian fissure." There are many facts which seem to show that Guldberg and Cunningham erred in their conception of the relation of these two areas :

1. The variations in the ventral extension of the central fissure are believed to be due to individual difference.

2. The connection of the central fissure with the Sylvian, when it occurs, is almost always by a small, variable opercular fissure (Cunningham 14, 341-2). Wilder, in 1894, in the report on the brain of an educated suicide, having apparently duplicate central fissures, says (65, 2): "On the left both centrals enter the Sylvian, with a depth of at least 5 mm. On the right, the first central approaches the precentral, the second joins the Sylvian at a depth of about 3 mm." So far as the writer has been able to learn, this connecting fissure never completely divides the operculum nor interrupts the circuminsular fissure in an otherwise normal brain.

3. The absence of the central fissure has not been shown to produce an appreciable effect upon the transinsular and if either is absent it is more often the central fissure.

4. The insula is always sharply defined and is believed to be a distinct lobe as sharply demarcated from the surrounding areas as any lobe of the cerebrum, and the fissures and

gyres upon its surface are also distinct and not dependent upon those of the rest of the cerebrum.

5. The central fissure is not known to exist outside of the primate brain, while, as will be shown, the transinsular fissure is present in many imprimates and the relation of the transinsular to the Sylvian in them is sometimes as in man (see raccoon); but more often it coincides in position and direction with the Sylvian fissure.

6. The transinsular fissure gradually becomes less deep as it approaches the circuminsular fissure dorsad, and it has never been shown to extend beyond this fissure, while in some imprimates it never reaches the dorsal margin of the circuminsular fissure.

7. The central fissure is sometimes double; the writer has been unable to find a single recorded instance of the duplication of the transinsular fissure.

8. The reasons given by Cunningham (13, 287) to show that because the preoperculum is (as he thinks) absent in the anthropoid it necessarily follows that a portion of the insula is also absent, are not well founded. The human insula has nearly or quite the same form before as after the appearance of the preoperculum and the writer fails to see why it should be otherwise in the ape.

9. The mononym "transinsular" fissure (Wilder) indicates better the relation of this fissure to the insula and is far preferable to the polyonym "sulcus centralis Reilii" of Guldberg and Cunningham.

The blood-supply of the insula is derived from the branches of the medicerebral artery which ramify over its surface. The main branch lies in the transinsular fissure as shown in Fig. 4. From these branches small arteries penetrate the cortex directly.

THE RELATION OF THE INSULA TO THE CLAUSTRUM.

On account of its intimate connection with the brain-stem, the insula has been called the stem-lobe or *Stammklappen*. Entad of the insular cortex (see Fig. 6) but separated from it by

a band of myelinic fibers, lies another cellular area called the claustrum (Burdach). These fibers, says Meynert, have their origin partly from the subfrontal gyre and partly from the uncus from which they radiate in a fan-shape separating the areas referred to above. The same author also says (37, 674): "The fibers of the *fasciculus uncinatus* traverse freely the substance of the claustrum as well as that of the *nucleus amygdalæ*. The anterior cord-like and hook-shaped part of the *fasciculus uncinatus* is joined by bundles of fibers distributed, as it were, in layers which pass through and along the surface of the claustrum, constituting an important part of the medullary substance of the island (of Reil) and of the external capsule."

In 1889 Spitzka (56, 172) said the claustrum "corresponds in extent nearly with the extent of the insula."

Obersteiner in 1890 (42, 68) said of the claustrum, "its lateral surface adapts itself to a certain extent to the cortex of the island of Reil, exhibiting similar small elevations and depressions."

Until recently, the claustrum has been assumed to be peculiar to the primate brain, and was an object of much speculation; but the researches of Betz, Meynert, Duret, Browning and others seem now to prove beyond a doubt that it is really a part of the insula which became separated from the cortex proper by the growth of the fibers referred to above. In 1879 Richet (48, 23) wrote: "It appears that in the brains of idiots, the white lamina, which separates the insular convolutions from the *avant-mur* is absent, and the *avant-mur* really becomes the internal layer of the cortex cerebri (Betz)." The same author (48, 24) quoting from Duret, says the circulation is the same as that of the insula. Browning in 1889 (5, 234) agreed with Duret and stated that the blood supply of the claustrum passed through the cortex of the insula and not through the *precibrium* (anterior perforated space). This being established it would seem that the presence of a claustrum was indicative of the presence of an insula. It also suggests the possibility of these fibers passing so far entad as not to demarcate a claustrum as is probably the case in the sheep. The former inference regard-

ing the presence of a claustrum indicating the presence of an insula at first seemed plausible but later reflection has caused the idea to be abandoned (see discussion under Carnivora).

THE INSULA IN THE PRIMATES OTHER THAN MAN.

The anthropoid apes, which in structure are so closely allied to man, possess a well developed insula.

Leuret and Gratiolet seem to have been the first to recognize this area. They say (31, II, 112): "Le lobe central paraît particulier à l'homme et aux singes, peut-être voit-on quelque chose d'analogue dans les makis, mais on ne voit rien de semblable chez les autres mammifères."

In 1891 Cunningham (13, 287) said: "One of the most remarkable characters in the cerebrum of the orang and the chimpanzee is the total absence of the frontal and orbital opercula. The temporal and fronto-parietal opercula are alone present." There is some diversity of opinion as to the entire "absence" of the suboperculum in these brains and Cunningham also admits the presence of a fissure which forms the cephalic boundary of the operculum but he does not believe it homologous with the presylvian fissure and hence does not recognize a suboperculum. Cunningham (13, 287) also says: "It is curious that while the anthropoid should be so absolutely destitute of a frontal and an orbital operculum, there are many of the lower apes (e. g. baboons, macaques, etc.) which show a faint trace of the orbital operculum."

In 1880 Parker, (46) stated that the insula of the chimpanzee "is well developed and is marked by several conspicuous radiating convolutions (gyri breves, Gall) and lies entirely concealed beneath a well-developed operculum."

In 1877 Major (34, 46) said the insula was relatively as well as absolutely smaller in the chimpanzee, etc., than in man.

Hartmann (26, 195) in 1886 wrote that "In the gorilla, chimpanzee, and orang, the island of Reil is generally—at least, according to my experience—overlapped by the operculum, although there are instances in which this is not the case."

In 1878 Broca (4, 645) said the insula of the gorilla bears "three gyres as in the orang, while there are four in the chimpanzee." Chapman in 1879 (8, 61) said: "The central lobe, or island of Reil, which is very slightly convoluted, is entire concealed in the chimpanzee."

Spitzka (56, 255) says that the gyres of the orang's insula correspond as to their direction and relations to those of man, though less marked. He further states that "in every anthropoid dissected by myself, I find these gyri and sulci; and one sulcus is a constant feature of even the *Cynocephali*."

The specimen here shown (Fig. 7) does not exhibit an area so well marked as those described by the above authors and this is probably due to the undeveloped state of the chimpanzee brain at this age. Excepting the circuminsular, the fissures of the insula are very rudimentary and few in number. This insula was entirely concealed within the Sylvian fissure. There seems to have been a feeble attempt at producing a transinsular fissure but no apparent approximation to a pole. Broca (4, 369) says: "L'insula est toujours simple chez les cèbiens et les pithéciens, ainsi que chez gibbons. Chez les grands anthropoïdes et chez l'homme, elle se subdivise en un certain nombre de plis qui convergent vers le pôle et vont gagner successivement les divers points de la rigole supérieure, qu'ils traversent pour se jeter profondément dans le lobe frontal."

Marchand (36, 1893) says: "In the lower apes the isle of Reil is exposed. This is the case in microcephalic idiots."

Spitzka (56, 173) has shown that the claustrum is present in the baboon and that it is similarly located to that of man.

The insula of the macaque monkey (Fig. 8) shows a well rounded eminence deeply imbedded in the Sylvian fissure. It is sharply demarcated by the circuminsular fissure but is otherwise unfissured and is about twice as long as broad.

Cercocobus fuliginosus presents an insula very similar to that of the macaque. It, like the last-named, shows a well-rounded eminence and a well-defined circuminsular fissure. The insula was deeply imbedded in the Sylvian fissure.

There are several lemurine brains in the Cornell Museum,

but they were not available for examination at the time this thesis was prepared.

In 1866, Flower (21) said of the Javan loris (*Stenops javanicus*) on separating the lips of the Sylvian fissure "no distinct median lobe, or insula, could be traced." The same author also says "In the sulci of the outer face in the lemur, the Sylvian fissure is deeper especially at its anterior or lower part and conceals a small but distinctly marked insula or median lobe."

ORDERS CHEIROPTERA AND INSECTIVORA.

The specimens belonging to the above named orders, so far examined by the writer, showed no evidence of a macroscopic insula.

THE INSULA IN THE CARNIVORA.

The area which represents the insula in this order is, in general, not well developed, but in a more or less rudimentary form may be said to be fairly constant. As a macroscopic area, however, I have been unable to recognize it in the domestic cat, the Angora cat, *Lynx rufus*, the ocelot (*Felis pardalis*), the skunk (*Mephitis mephitis*), the mink (*Putorius vison*) and the ferret (*Putorius domestica*). My observations made in the latter part of 1893 upon the seal (*Phoca vitulina*) agree with the conclusion of P. A. Fish (20 ½, 16, 1896) who has shown that the Sylvian fissure has not suffered any marked displacement and that Spitzka (1890, *American Naturalist*, XXVI, 115-122) erred in assuming a vertical communicating fissure (*v. f.* Fig. 9) as the true Sylvian. The position of the insula shows conclusively that the caudal one of these two fissures is the true Sylvian. Dr. Fish also says: "The vertical and the true Sylvian fissures meet superficially at the latero-ventral angle of the cerebrum and if the sides of the Sylvian be separated, it will be seen that the vertical fissure instead of directly joining the Sylvian becomes a submerged fissure . . . and crops out again on the ventral surface on the front or cephalic wall of the mouth of the Sylvian. . . . This condition is found on both sides." The insula is repre-

sented in the seal (*Phoca vitulina*) and the panther (*Felis concolor*) in Figs. 9 and 10 respectively. In each the area is devoid of fissures except the circuminsular, thus indicating its very rudimentary character. The area is only slightly elevated and was entire concealed within the Sylvian fissure. It is present and of about the same rudimentary character in the hyena where it is flatter than in the preceding and is entirely concealed. It is concealed and rudimentary in the lion. In 1879 Pansch (45, 166) said that it is present but concealed in the fox.

Fig. 11 represents this area in the raccoon. The circuminsular fissure is interrupted at two points leaving the insula joined to the temporal lobe caudad and the cephalic boundary ill defined. This elongated and flattened area is crossed by a fissure which is believed to represent the transinsular, although it does not correspond exactly with the direction of the Sylvian (see Fig. 12), as is usually the case in the imprimates at least. Nevertheless it almost completely divides the area into a pre-insula and a postinsula, is deepest at its junction with the rhinal and at that point it corresponds in position with the Sylvian. This lack of conformity is strongly suggestive of a displacement of the Sylvian fissure as the result of growth in an inclosed space which may have carried the dorsal end of the Sylvian caudad while the bounding parts of the ventral end, which is more closely connected with the brain stem, have maintained their original position. Future investigation may also show that some peculiar development of the frontal or parietal lobes or of both has aided in bringing about this condition. The relation of the transinsular to the Sylvian fissure in this brain is strikingly similar to that in the human, but in the raccoon there is no evidence of the central fissure. The area is otherwise unfissured, but slightly elevated and, with the exception of the cephalic third which lies concealed in the Sylvian fossa, it is completely hidden within the lips of the Sylvian fissure. As previously stated, the cephalic boundary is ill defined and the insular area graduates out into the frontal lobe as in the case of young pigs. The plane (plane of fissured surface) of the insula in this specimen forms an angle of more than 45° to the lateral

surface while that of the seal, panther, hyena and most primates is nearly parallel to the lateral surface.

The insula of the Thibet bear (*Ursus thibetianus*), Fig. 13, is very different in its appearance from the preceding—as if, instead of the prolonged growth caudad, as in the raccoon, the surrounding areas which presumably have reached a higher state of development, had produced a cephalo-caudal compression of this area, resulting in the formation of two parallel gyres separated by the transinsular fissure. Relative to the length of the cerebrum, the insula in this specimen is much shorter than that in the raccoon. The transinsular fissure here is deep and coincides very closely both in direction and position with the Sylvian. The area is sharply demarcated by the circuminsular fissure except at the cephalic end where a slight depression probably marks the cephalic boundary. The area is well rounded and the plane of the insula is parallel to the lateral surface. The insula was not wholly concealed, a small portion of the caudo-ventral end of the cephalic subgyre being visible before dissection. The area was almost entirely within the Sylvian fissure. In 1888 Turner (59, 566) said: “In the brain of the Polar Bear, I have shown that an entire arched convolution is concealed within that [Sylvian] fissure.”

This area in the dog (*Canis familiaris*) is situated normally at the bottom of the Sylvian fissure and is entirely concealed. The plane is parallel to the lateral surface or nearly so. It is a well rounded, oval area somewhat triangular in form, is sharply defined by the circuminsular fissure and, as stated by Huxley, is usually unfissured. Figs. 14 and 15 represent an exceptional condition. The insula was exposed on both sides and was situated almost wholly in the Sylvian fossa. The area was well rounded and its outline approximately rectangular. Another peculiar specimen is shown in Fig. 16. Here the insula, while entirely concealed within the Sylvian fissure, was crossed by a fissure which may represent the transinsular fissure and if so the preinsula is the smaller. In order to determine with greater certainty the nature of this fissure the area was removed and sectioned. The shallowness of the fissures (Fig. 17) plainly

shows that the fissure crossing this area is not a part of the circuminsular but an independent fissure, probably the transinsular as previously stated. The small area cephalad undoubtedly represents a preinsula. Owing to the normally simple character of this area in the dog, these individual differences are very striking.

A transection of the cerebrum of a dog is shown in Fig. 18. The insula appears as it normally exists concealed by the overlapping portions of the temporal and parietal lobes. The myelinic fibers of the olfactory tract readily distinguish the rhinal fissure and it will be noted that they do not extend beyond the bottom of this fissure. A band of myelinic fibers extending apparently from the dorsal overlapping area of the parietal lobe, passes through the insular cortex cutting off the ental layers which constitute an area probably homologous with the claustrum. The study of sections caudad of this one shows that this band of fibers ventrad of the insula bends around into the temporal lobe. It would thus appear that a part of them at least might be association fibers. Fibers also given off from this band are distributed through the claustrum. Myelinic fibers are also found in the ectal dense layer of cortex of the insula and they extend for the most part parallel with the surface.

The insula receives its blood-supply directly from minute branches of the medicerebral artery, which pass in from the surface and which are seen in longisection in Fig. 18. The writer has been unable in most cases to determine the origin of vessels found in the claustrum as they were seen only in transection. A few however have been found which passed directly across the area as in the case of the one represented in the dorsal end of the claustrum. These would seem to indicate that a part of the supply might be received directly from the surface arteries. In the vicinity of the fiber tracts, arteries, in general, seem to follow the direction of the length of the fibers and not to cross them.

As previously stated, no macroscopic area appears at the bottom of the Sylvian fissure of either the cat (see Fig. 19) or the

skunk (Fig. 20). In each the width of the Sylvian fissure is practically the same throughout its length and at the bottom as near the surface. The study of many transections of the Sylvian region confirms the statement that there is no marked widening of the Sylvian fissure at any point ; there is absolutely no sign of a circuminsular fissure and consequently no evidence of an ectal area homologous with the insula. Recourse was then had to the Weigert method with the result that it has been demonstrated in each that a cellular area had been separated from the cortex entad of the Sylvian fissure by a thin lamina of myelinic fibres. This area is similarly situated to the claustrum of the dog and in the skunk at least the fibers appear to arise from the area dorsad of the Sylvian and pass to some area ventrad or *vice versa*. In the cat, however, this lamina appears to connect the area ventrad of the Sylvian fissure with the central mass of myelinic fibers rather than with the area dorsad of the Sylvian. The origin of these fibers does not effect the question as to whether or not this is really a claustrum for, while it is known that fibers from the uncus and subfrontal gyri pass entad of the insula and assist in the demarcation of a claustrum in the human brain, it is not known but what fibers having a different origin also take part. Certain it is that if these myelinic fibers (which appear to be of the association type in the dog and skunk) were not there this area would remain a part of the cortex as has been shown is sometimes the case in the human brain. The fibers which make up this lamina are much fewer than in the dog and the number is still less in the skunk than in the cat. Some twelve days after I had thus independently reached the conclusion that this area was homologous with the claustrum, my attention was called by Professor Wilder to an article by Graeme M. Hammond, in 1881 (26). This article contains figures showing that the author had noticed the area in the cat, sketched it though imperfectly and named it the claustrum. In 1889, Spitzka (56, 173) also figured this area in the cat but did not name it. The writer was unable to recognize a claustrum in (Weigert) transections of the brain of the mink. This animal has no Sylvian fissure.

The significance of the presence of the claustrum is difficult to determine. As previously stated, the existence of a claustrum might, in general, be taken to indicate the presence of an insula but such is not believed to be true in either of these instances. Presumably if a rudimentary insula did exist in the cat, then only a small portion of the claustrum would correspond therewith; and if only a part of the claustrum belongs to this area, then, as in this case where the claustrum is of considerable size, the larger part of the claustrum has necessarily no connection with the insula. Indeed it might exist quite as well without an insula. Hence it would appear that the only significance attached to the presence of a claustrum in such cases is that the cortex at the bottom of the Sylvian fissure is relatively farther ventrad than in those brains where the area is not so demarcated, as in the sheep and mink.

Turner in 1888 (59, 566) said: "In the true carnivora, the Sylvian convolution was, as a rule, superficial and on the cranial aspect, though in the otter and badger indications of the depression of its anterior limb within the fissure were seen. In the seals and walrus, the concealment of this convolution was still more marked, so that the brains of these animals form apparently, in this particular, a transition to those of man and apes, in which the concealment of the island is complete."

THE INSULA IN THE PROBOSCIDA.

In the single specimen of the Indian elephant examined by the writer, the insula (Fig. 21) is only slightly developed. It consists of an almost flat area in the bottom of the Sylvian fissure and is made up of three gyres, two of which belong to the postinsula. This disposition of the insular area suggests that in the unusual dog (Fig. 16) except that in the latter the postinsula is at the same time more elevated. In the elephant the postinsula contains the greater number of gyres but the preinsula is the more elevated. The entire area is deeply imbedded in the Sylvian fissure and extends ventrad as far as the rhinal fissure. This observation is contrary to that of Owen, 1868, who declares (44, 129) that "the minor inter-Sylvian con-

volutions are exposed in the sheep and elephant." He also says (44, 123) "It is well marked and rises high up the Sylvian fissure in the Proboscidiens." In 1879 Spitzka (52) said that the insula in the elephant is completely covered. The largest branch of the medicerebral artery lies in what I have called the transinsular fissure but this artery does not reach the dorsal margin of this area. At about one-half or two-thirds of the distance from the ventral boundary of the insula, the artery leaves the area to pass dorsad into the Sylvian fissure. This peculiar condition seems to have been brought about by the very unusual growth of the area dorsad of the insula, which fold has been projected ventrad as a rudimentary subopercular fold.

THE INSULA IN THE RODENTIA.

None of the members of this order so far as examined by the writer showed any evidence of a macroscopic insula. Transsections of the Sylvian region prepared by the Weigert method failed to show the presence either of an insula or a claustrum in the woodchuck.

THE INSULA IN THE UNGULATA.

With the exception of the primates, members of this order seem in general to have reached a higher state of insular development than those of any other order, a significant fact when it is considered that this order is usually placed so far down the list on account of other characters. The specimen of the camel here shown (Fig. 22) can hardly be taken to indicate much more than the existence of an insula in this animal. The area is nearly flat and presents no fissures other than the circuminsular. The insula is proportionally very small and shows on the whole a rudimentary state of development compared with the surrounding lobes. It was completely concealed within the Sylvian fissure, the ventral end scarcely reaching the rhinal fissure; the wider end of the insula is dorsal. It is concealed and rudimentary in the bactrian camel (*Camellus bactrianus*).

The deer (No. 961) presents a well defined area and at the same time one not indicating a high degree of development. The insula (Fig. 23) was completely concealed and is situated

almost wholly in the Sylvian fossa, only the caudal end extending dorsad into the Sylvian fissure. With one exception the fissures are merely broad shallow depressions which indicate a tendency to divide the area into five gyres. The caudal fissure probably represents the transinsular and is the only one indenting the lateral surface of this area. The plane of the insula is nearly perpendicular to the lateral surface; the surface is well rounded and throughout its entire length lies just dorsad of the olfactory tract. The insula is present also in the fallow deer (*Cariacus clama*) and exposed on both sides. At least three fourths of the insula is cephalad of the ventral end of the Sylvian fissure. The transinsular fissure is rudimentary on the left side but better developed on the right. The difference in the position, relative development, form, and relations of the insula in the camel and deer are very great and more marked than one might expect in animals so closely related.

The area which represents the insula in the sheep (Figs. 32-33) is, contrary to the rule, exposed. It is probably due to this fact that this area has not previously been treated by writers on the sheep brain. Only Leuret and Owen seem to have recognized it. The former states that, except in the sheep, they [supplementary convolutions] are found "only in the brains of man, elephant and monkeys." Owen says: "the minor inter-Sylvian convolutions are exposed in the elephant and sheep."

This area, as has been rightly said, is exposed in the sheep and throughout its length lies just dorsad of the olfactory tract in the Sylvian fossa. The rhinal fissure which separates these areas is always well defined. In adults the lateral exposed surface is usually indented by two (apparently three) fissures—the most cephalic and caudal being found upon dissection to be parts of the circuminsular, while the median one is the lateral outcrop of what the writer considers the homologue of the transinsular fissure. Other indentations are frequently noticed but they are usually slight and are probably caused by pressure of branches of the medicerebral artery which lie in them. Upon dissection, it becomes evident from the greater fissuration

that the dorsal and not the lateral surface is homologous to the lateral areas of most mammals and that the plane of the insula is perpendicular to the lateral aspect. Presumably in this brain as in the human the circuminsular fissure is the first developed and in adults is usually complete. In younger specimens however it is quite noticeable that this fissure is interrupted in one or more places as on the lateral surface at the cephalic end of Fig. 32 and at the dorso-caudal boundary of Fig. 33. With the exception of the circuminsular but one fissure of this area appears to be constant and is the only one extending upon the lateral as well as the dorsal surface. This fissure is continuous with the rhinal; in it lies the largest branch of the medicerebral artery which passes dorso-mesad into the Sylvian fissure; it coincides throughout most of its course with the direction of the Sylvian, divides more or less completely the area into a preinsula and a postinsula and is the fissure which, in the discussion of the lateral surface, was called the transinsular fissure. This branch of the medicerebral artery after traversing nearly two thirds of the length of the transinsular from the lateral surface mesad suddenly leaves it and passes up into the Sylvian fissure, thus giving the appearance as if the nearly equilateral triangular caudo-mesal portion of the caudal gyre of the preinsula had grown caudo-ventrad of the artery. Presumably what has happened is that a displacement of the Sylvian fissure has occurred due to a greater development of the temporal or occipital lobes than the frontal and parietal; that this growth in an inclosed space has resulted in carrying cephalad the dorsal end of the Sylvian and with it the artery, thus removing the artery from the mesal end of the transinsular, where presumably it originally was lodged. The vertical position of the Sylvian fissure would seem to indicate that such a displacement had occurred. The relation of the Sylvian to the transinsular fissure is very striking when compared with that in the raccoon, where the Sylvian was mostly caudad of the transinsular. In two instances only have fissures other than those above mentioned been seen on the lateral surface of the sheep brain and in each case, as might be expected, they were in the preinsula.

The dorso-lateral aspect (Fig. 33) shows the preinsula to consist of three gyres while the postinsula has but one. The gyres of the insula are in general simple. One specimen, however, showed the caudal gyre (postinsula) subdivided into three parts. The fissures grow deeper as they approach the meson except the transinsular but it is not known that any are constant. The sheep brain exhibits two unusual conditions shown in the transection of this brain (Fig. 34): first, that a bundle of myelinic fibers enters the insula from which it might be inferred that this area is functional, or at least assists in the performance of a function. These fibers seem to pass principally to the dorso-lateral part of this area, although it is evident that many are given off along its course to other parts of the area mostly dorsad. Secondly, there is no indication of a claustrum. It is not believed that any great significance can be attached to the apparent absence of this part in the sheep other than that the insula in this animal is relatively farther laterad than in those where the claustrum becomes so demarcated and hence the fibers from surrounding areas which in some other animals pass through the cortex here pass wholly mesad. The blood supply is derived wholly from branches of the medicerebral artery which extend over the surface. The position of the rhinal fissure and the relations of the insula to the olfactory tract are clearly shown. The myelinic fibers of the latter extend only to the bottom of the rhinal and in no case have fibers been found extending upon the insular area. This fiber area of the olfactory tract extends considerably farther ventrad than shown (Fig. 34) and at the ventral end the fibers are most numerous and collected into a bundle of considerable size.

The insula of the cow (Figs. 26-29) is well developed, exposed on the lateral aspect and lies almost wholly within the Sylvian fossa. It presents in this animal peculiarities not previously met with. The area in but one of five specimens was completely divided into a preinsula and a postinsula. In this one (3362) the transinsular fissure was well marked, was deepest at the latero-ventral end, and was continuous mesad with the circuminsular. The fissure cephalad of the transinsular also

completely crossed the insula but was shallow at the ventral margin. The area is more often incompletely divided by the transinsular fissure which, while it is of considerable length and depth, is almost always confined to the lateral surface. The part most elevated in the five specimens examined lies in the postinsula always directly caudad or caudo-mesad of the dorsal end of the transinsular fissure. What has been assumed as the plane of the insula is at an angle somewhat greater than ninety degrees with the lateral surface. The caudal and caudo-lateral surfaces of this elevated portion slope very abruptly from the apex of this elevated portion to the temporal lobe. The slope toward the mesal boundary is always more gradual and becomes still more so as the cephalic boundary is approached. A curious condition exists at the caudal end of the preinsula where, on the lateral surface, the appearance is as if a quite successful effort had been made to tuck that part caudo-mesad under the postinsula. This is more marked on the left side (see Fig. 26) than on the right (Fig. 27), and the crowded appearance of this area seemed more marked in adult than in younger specimens. The surrounding lobes appear to be well developed, while the olfactory tract is enormous. The study of this brain seems to confirm the impression that these remarkable features are due to growth in an enclosed space. The insula shows the effects of compression in a marked degree.

The circuminsular fissure of the right side (Figs. 27-28) sharply defines the insular area except at the temporal lobe where the fissure is interrupted and a junction of the insula with the temporal lobe is formed at the lateral surface. This insula consists of seven gyres only one of which belongs to the postinsula. On the left side of the same specimen (Figs. 26 and 29) the circuminsular fissure is also interrupted with the formation of a similar junction as on the right side. Two interruptions of the circuminsular are found at the cephalic margin on the left side. The dorsal surface is divided into four gyres, three of which belong to the preinsula. A zygal fissure¹ (Fig. 29, *zf*) exists near

¹ See Wilder (64, 155).

the middle of this area, the base extending in the direction of the length of the area. While this surface is much less fissured than the corresponding surface of the right side, the lateral surface of the left side appears much more complicated. In the left insula of the cow (3137) the transinsular fissure was wholly exposed on the lateral surface; there was no interruption of the circuminsular at the cephalic margin, and the dorsal surface presented five gyres, four of which belong to the preinsula.

In 1890, Turner (61, "Fig. 26") gave a wrong idea of the Sylvian fissure (see Fig. 30) in the cow. He mistook the transinsular fissure for the Sylvian.

In the insula of the cow, individual and lateral variations are perhaps more marked than in that of any other animal examined. We have here exemplified also the peculiar folded appearance first noticed in the bear but more marked.

The area representing the insula in the burro (*Equus asinus*) is better developed than that in the deer. It is well rounded and, except at two points along the cephalic boundary, the area is sharply defined by the circuminsular fissure (Fig. 24). As in the deer, the area is divided into a preinsula and a postinsula by the transinsular fissure, the latter area containing but one, while the former consists of four gyres all well developed and sharply defined. There is no approximation to a pole as in man. The location of the area is similar to that of the deer, only the caudal one third lying in the Sylvian fissure. The two most cephalic gyres of the preinsula were exposed before dissection and the plane of the area makes an angle of not more than 60° with that of the lateral surface.

In 1871, Lussana and Lemoigne (33) stated that the insula of the horse was of considerable size. The writer has examined five brains, two of which, at least, are worthy of description. The first was that of a work-horse (2777, R. half) which showed five gyres exposed previous to dissection. Upon dissection the plane appeared almost perpendicular to the lateral surface, the gyres were six in number and the fifth (from the cephalic end) was subdivided by a small fissure at the mesal end. The fissure separating gyres 2 and 3 is deep, extends

over the dorsal surface and almost completely divides the pre-insula upon the lateral surface.

The insulas of the "Sage horse" (Fig. 25) consist of five gyres each, of which three belong to the preinsula and two to the postinsula. Before dissection the left insula showed four gyres exposed while the right showed three. One of the main branches of the medicerebral artery lies in what I have called the transinsular fissure (Fig. 25). This fissure is well marked on both sides. In the left insula the two most cephalic gyres are nearly perpendicular, while the other three are at an angle of about 60° to the lateral surface. On the right all the gyres are in about the same plane which lies nearly perpendicular to the lateral aspect. Those of the postinsular seem better developed and the first gyre of the postinsula is the one most elevated. There seems to be an approximation to a pole in this specimen not found in any other animals than the primates. The second gyre is also the smallest as in man.

The insular region of the tapir (*Tapirus malayanus*, Fig. 31) presents a very peculiar appearance, from the fact that between the area which I have called the insula and the rhinal fissure there seems to have arisen a corrugated area which is not believed to belong to the insula at all. This area extends from the frontal to the extreme end of the occipital lobe and throughout its course lies just dorsad of the rhinal fissure which is interrupted at several points on the left side but is continuous on the right. The fissure dorsad of this area is nearly parallel to the rhinal except near the caudal end. The area included between these two fissures is fissured, but only slightly elevated above the olfactory tract, and is continuous with the insular area. The insula in this specimen is only slightly elevated and contains but two gyres of which the more cephalic is the larger. The fissures are simple and very shallow except the circuminsular at the cephalic end. The transinsular is not well marked near the mesal margin. The insula is entirely concealed.

In 1878 Krueg (30, 325) said the insula was present in the Hippopotamidæ. Chapman in 1881 (9, 144) said: "The

Sylvian fissure in my Hippopotamus is quite evident and within it I noticed a rudimentary island of Reil."

THE INSULA IN THE CETACEA.

Fig. 35 represents the insula of the porpoise (*Globiocephalus melas*). In this specimen the insula is completely concealed within the Sylvian fissure and the plane is parallel to the lateral surface. The area is proportionally very large but at the same time very flat and there is no evidence of a fissure homologous with the transinsular and no approximation to a pole. This specimen shows at least nine gyres, three of which are subdivided by fissures which are deepest near the circuminsular. It is not known that any of the fissures of this area are constant. In 1879 Spitzka (53) says the "insula in the porpoise has four times as many convolutions and is twice as large as that in man and is completely covered by the operculum and temporal lobe." The same author also says that one specimen in his possession has either thirteen or fifteen gyres. Wilder [lecture] said that the gyres of the porpoise insula exceed in number those of any other mammal observed by him, but they are smaller, and he concluded that "in combined elevation and fissuration, the insula reaches its highest development in man."

Ziehen (31, 110, 1889) says of the white whale (*Beluga lucas*), "The area between the fissura circularis interna and the fissura circularis externa, probably also a large part of the covered portion of the floor of the Sylvian fossa ought to be designated as insula." Of the Sylvian fissure in *Megaptera boops*, he (31, 125) says "Ursprung vom aus der Fissura Rhinalis Anterior. Die Haupttheil bildet die obere Begrenzung des Inselndreiecks."

None of the representatives examined of the remaining orders show any evidence of an insula.

SUMMARY.

1. Neither the insula nor the claustrum is constant among mammals.

2. The insula is present in the Primates, Carnivora, Proboscidea, Ungulata and Cetacea. It is apparently absent in the Cheiroptera, Insectivora, Rodentia, Sirenia, Marsupialia and Monotremata.

3. The claustrum may include parts of areas other than the insula.

4. The insula and the claustrum may generally be considered as parts of the same cortical area; the claustrum may be present without the insula; both may be present or both may be absent.

5. The apparent absence of the claustrum when the insula is present indicates that, relative to the surrounding areas, the insular cortex is farther laterad than in those specimens where it is so demarcated. The myelinic fibers of the surrounding areas then pass wholly entad of the insular cortex.

6. The insula is, in general, a convoluted area.

7. The insula is sometimes a *subarea* but quite often it is exposed upon the lateral surface of the cerebrum.

8. The exposure of the insula may indicate either its own excess or the deficiency of the overlapping adjacent parts.

9. The gyres of the overlapping areas are always intercalated with those of the insula.

10. Individual and lateral variations upon this area are numerous and marked and are probably due in part to growth in an enclosed space.

11. The insula in the Primates, the Carnivora, some of the Ungulata and Cetacea and perhaps others is a subarea or subgyres at the bottom of the Sylvian fissure.

12. The insula frequently is almost wholly within the Sylvian fossa. This condition is not believed to indicate in any way a different relation to the parts entad but rather a more uniform development of the insula and the surrounding areas so that no lateral overlapping has taken place and hence the ventral end of the Sylvian fissure remains unclosed as a fossa.

13. The insular area, in the more generalized types of mammals, at least, does not belong primarily to the rhinencephalon as held by Turner in regard to the human brain.

14. The fissured surface which is usually the dorsal in the raccoon, the deer, the burro, the horse, the pig, and the sheep, is homologous with what appears on the lateral surface of the insula of the Primates, most of the Carnivora and some others.

15. The variation in the plane of the fissured surface of the insula is probably due to some peculiarity in the development of the brain stem.

16. Fissures on the insula are less deep and more open than on the surrounding parts; this is probably due to growth under pressure of overlapping parts.

17. The lack of conformity between the Sylvian and transinsular fissures both in position and direction is probably due to the mechanical effect of growth in an enclosed space by which a displacement of the Sylvian has occurred.

18. The difference in the relative mass of the insula, its position, plane and relative development in the camel and deer is very much greater than might be expected in two animals so closely related.

19. The difference between the insula of the bear and the raccoon is very striking.

20. It is noteworthy that the cat (*F. domestica*) and ocelot (*F. pardalis*) and the lynx have no insula, while the panther (*F. concolor*) and the lion (*F. leo*) have a rudimentary one.

21. The overlapping of the insula in the human brain, and presumably in others, is not due to a cessation of growth of the insula but to the more rapid growth of the surrounding lobes and the rapid enlargement of the paracœles.

22. The apparent approximation to a pole in the horse is noteworthy.

23. The primitive insula, if such exists, is a somewhat elevated area of greater or less size surrounded by a circuminsular fissure and located in the Sylvian fossa or in the fissure if the fissure is continuous with the rhinal.

SYNONYMY—INSULA.

1. Central lobe.—The application of this term to the insula is objectionable on account of its more common use in connection with a lobe of the cerebellum and also because the adjective, central, is often applied to fissures and lobes topographically related to the central fissure (f. of Rolando).

2. Convolutions placed between the fissure of Sylvius and the corpus striatum (Vicq d'Azyr).

3. Circonvolutions supplementaires (Leuret and Gratiolet).

4. Entosylvian folds or tract (Owen).

5. Fifth lobe of the brain.

6. Gyri breves (Gall, Arnold).

7. Gyri aperti.

8. Gyri unciformes (Eberstaller).

9. Ile.

10. Insel (Reil).

11. Insellappen.

12. Insula. This name takes precedence over all others, being the Latin form of "Insel," the name given by its first describer, Reil. The regular paronyms of insula as given by Wilder (22, 530-31) are English, insula; German, Insel; French, insulé; Italian, isola.

13. Insula de Reil.

14. Insula del Reil.

15. Insular lobe.

16. Insula Reilii.

17. Insula Sylvii (Mingazzini).

18. Intersylvian convolutions (Owen).

19. Intralobular gyri (Quain).

20. Island of Reil (English Authors).

21. Isola.

22. Limen insulæ.

23. Lobe central (see note under 1).

24. Lobe central de l'insula (see note under 1).

25. Lobe de l'insula de Reil (Broca).

26. Lobe intermediaire.

27. Lobe moyen.

28. Lobettino centrale nel tipo pecorino (Tenchini and Negrini).

29. Lobo centrale (Gratiolet).

30. Lobo fondamentale (Lussana).

31. Lobo insulare (Lussana).

32. Lobule de l'insula.

33. Lobule du corps strié.

34. Lobule sous-sylvien (Broca).

35. Lobulo del corps striato.

36. Lobulo sotto-silvico (Tenchini and Negrini).

37. Lobulus centralis (see note under 1).

38. Lobulus corporis striati.

39. Lobulus fissuræ Sylvii.

40. Lobus caudicis (Burdach).
41. Lobus insulæ.
42. Lobus intermedius s. opertus.
43. Lobus opertus (Arnold).
44. Lobus retractus.
45. Median lobe.
46. Minor intersylvian convolutions (Owen).
47. Quinto lobo delle cervello.
48. Reil's island.
49. Stammlappen (Huschke).
50. Subsylvian fold (Owen).
51. Subsylvian lobe.
52. Subsylvian tract (Owen).
53. Versteckenlappen (Arnold).
54. Zwischenlappen (Arnold).

SYNONYMY—CLAUSTRUM.

1. Avant-mur.
2. Claustrum (Burdach).
3. External wall (Huguenin, Charcot).
4. Noyau rubané.
5. Nucleus tæniæformis (Arnold).
6. Rampart.
7. Rempart.
8. Vormauer.

SYNONYMY—TRANSINSULAR FISSURE.

1. Fissura interinsularis (Eberstaller).
2. Hauptfurche der Insel (Eberstaller).
3. Inselfurche (Eberstaller).
4. Le grand sillon de l'insula (Brissaud).
5. Sulcus centralis insulæ (Guldborg) 13.
6. Sulcus centralis Reilii (Turner).
7. Sulcus Insulæ (Eberstaller).
8. Transinsular fissure (Wilder).

SYNONYMY—CIRCUMINSULAR FISSURE.

1. Circuminsular fissure, (Wilder).
2. Fissura circularis.
3. Rigoles de l'insula (Broca).
4. Sulcus circularis Reilii (Schwalbe) 43.

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EXPLANATION OF FIGURES.

With the exception of figures 1, 2, 3, 4, 5, 6, 7, 8, 12, 17, 18, 19, 20, 21, 25, 31 and 34, all the figures were produced as follows: The specimens were photographed natural size, with a vertical camera; from the photographs out-

* The exact title of Reil's article is not known by the writer.

lines were traced also with the camera. Liability to distortion due to the enlargement of the parts of an uneven surface was materially reduced. Figures 1, 2, 3, 4, 5, 6, 7, 21, 25, 31, were photographed natural size and enlarged from photographs or figures as indicated, with an enlarging apparatus. Figures 8, 17, 18, 19, 20 and 34 were photographed as stated and traced from photographs. Fig. 12 was made from outlines traced from photographs of lateral views before and after dissection.

ABBREVIATIONS.

<i>art.</i> —artery.	<i>p. op.</i> —postoperculum.
<i>circ. f.</i> —circuminsular fissure.	<i>prein.</i> —preinsula.
<i>cl.</i> —claustrum.	<i>Preop.</i> —preoperculum.
<i>fl. olf. tr.</i> —myelinic fibres of olfactory tract.	<i>rh. f.</i> —rhinal fissure.
<i>in.</i> —insula.	<i>subop.</i> —suboperculum.
<i>op.</i> —operculum.	<i>Sy. f.</i> —Sylvian fissure.
<i>P.</i> —Pole of the Insula.	<i>tr. f.</i> —transinsular fissure.
<i>postin.</i> —postinsula.	<i>z. f.</i> —zygal fissure.
	<i>v. f.</i> —vertical fissure.

DESCRIPTION OF FIGURES.

The numbers are the serial numbers of the Museum of Vertebrate Zoology of Cornell University.

PLATE IX.

Fig. 1. Lateral aspect of the left half of the brain of a human fetus, size and age unknown. 2278; x 1 (after Wilder, 63, Fig. 4760).

Fig. 2. Ventral aspect of the left cerebrum of a human foetus, size and age unknown. 1820; x 1 (after Wilder, 64, Fig. 4782).

Fig. 3. Lateral aspect of right human insula, age and sex unknown, adult, 1805; x 1. The insula was exposed by cutting away the surrounding lobes down to the level of the circuminsular fissure, thus exposing the medicornu and hippocamp. The three eminences 1, 2 and 3 belong to the postinsula. The fissure marked 4 is too sharply outlined near the ventral end. At the point indicated it is a mere vasal furrow and does not communicate with the Sylvian fissure ventrad.

Fig. 4. Lateral aspect of right human insula, age and sex unknown, young, 1823; x 1. This preparation shows the branches of the medicerebral artery as it divides over the surface of the insula. The largest branch lies in the transinsular fissure for about two thirds of the distance across the insula, then leaves this fissure and bends caudo-dorsad as if towards the Sylvian. There is also shown a tendency toward the demarcation of an eminence similar to that shown in Fig. 3.

Fig. 5. Dorso-lateral aspect of the right human insula, age 37 years, male, 376; x 1. A nearly normal insula except for the unusually elevated pole, *P.* The short furrow cephalad is represented too deep and too narrow.

Fig. 6. Caudal aspect of a transection of the left cerebrum of man, after Wilder (64, 4732). Shows the relation of the insula to the claustrum, the brain stem and operculums.

PLATE X.

Fig. 7. Lateral aspect of the right insula of chimpanzee, supposed age 4 years, female, 265; x 1. The operculums have been cut away.

Fig. 8. Lateral aspect of the right insula of a macaque monkey, age and sex unknown; x 1. The lateral portion of the cerebrum was removed to the level of the ventral half of the circuminsular fissure. The remainder of the insula was exposed by cutting a groove parallel with the Sylvian fissure.

Fig. 9. Lateral aspect of the left insula of a seal (*Phoca vitulina*); x 1. Operculums cut away. The black areas at the dorsal and ventral ends indicate broken surfaces where the parietes were removed, and are too black.

Fig. 10. Lateral aspect of the left insula of a panther (*Felis concolor*), female, 18 years old, 309; x 1. Operculums cut away.

Fig. 11. Lateral aspect of the right insula of an adult raccoon (*Procyon lotor*), male, age unknown, 2031; x 1. The overlapping portions have been removed.

Fig. 12. Diagram of the same, showing the relation of the Sylvian and transinsular fissures.

Fig. 13. Lateral aspect of the right insula of a Thibet bear (*Ursus thibetianus*), male, age at least 5 years; 645; x 1. Shows well the relation of the transinsular and Sylvian fissures.

Fig. 14. Lateral aspect of insular region of a dog (cross between French poodle and Skye terrier), age more than 18 years, sex unknown, 166; x 1. Shows the exposure of the insula before dissection.

Fig. 15. Lateral aspect of the insula of the same with the operculums cut away; x 1½.

Fig. 16. Lateral aspect of the right insula of a dog (*Canis familiaris*), age unknown, probably adult, male; x 1.

Fig. 17. Outline of a section of the above looking dorsad; x 1. The dotted brace indicates the extent of the insula.

PLATE XI.

Fig. 18. Transection of the cerebrum of a dog (*C. familiaris*), male, age a few weeks, 3124; x 2½. Section made according to Weigert's method, after hardening the brain in 3% and 5% bichromate of potassium, imbedded in colloidal and cut in oil; differentiates alba and cinerea.

Fig. 19. Transection (Weigert) of a portion of the left cerebrum across the Sylvian fissure of a cat (*Felis domestica*), age and sex unknown; x 2½.

Fig. 20. Transection (Weigert) of a portion of the right cerebrum across the Sylvian fissure of a skunk (*Mephitis mephitis*), age and sex unknown; x 2½.

Fig. 34. Transection of the right insular region of a sheep (*Ovis aries*), age and sex unknown, looking cephalad; x 4½.

PLATE XII.

Fig. 21. Lateral aspect of the left insula of an elephant (*Elephas indicus*), age unknown, female, 2181; x 1. Overlapping portions have been dissected away.

Fig. 22. Lateral aspect of insula of a camel (*Camelus dromedarius*), male, age 15 minutes, 2122; x 1. The shaded portion at the right of the insular area is a broken surface and does not belong with the insula.

Fig. 23. Lateral aspect of the left insula of a deer (*Cariacus virginiana*), male, age unknown, 961; x 1.

Fig. 24. Lateral aspect of the left insula of a Mexican burro (*Equus asinus*), male, age unknown, 2259; x 1.

Fig. 25. Lateral aspect of the left insula of a horse (*Equus caballus*), male, adult, 2095; x 1.

Fig. 26. Lateral aspect of the left insular region of a cow (*Bos taurus*), adult, sex unknown, 3408; x 1. Shows exposure of the insula.

Fig. 27. Lateral aspect of the right insular region of a cow (*Bos taurus*) adult, sex unknown, 34c8; x 1. Shows exposure of insula before dissection.

Fig. 28. Dorso-lateral aspect of the right insula of the same, exposed by cutting away the operculums.

PLATE XIII.

Fig. 29. Dorso-lateral aspect of the left insula of the same after dissection.

Fig. 30. Lateral aspect of the cephalic half of the left cerebrum of a cow (*Bos taurus*), after Turner (61, Fig. 26). The fissure marked S, which Turner considers as the Sylvian, is the transinsular; the Sylvian is directly dorsad.

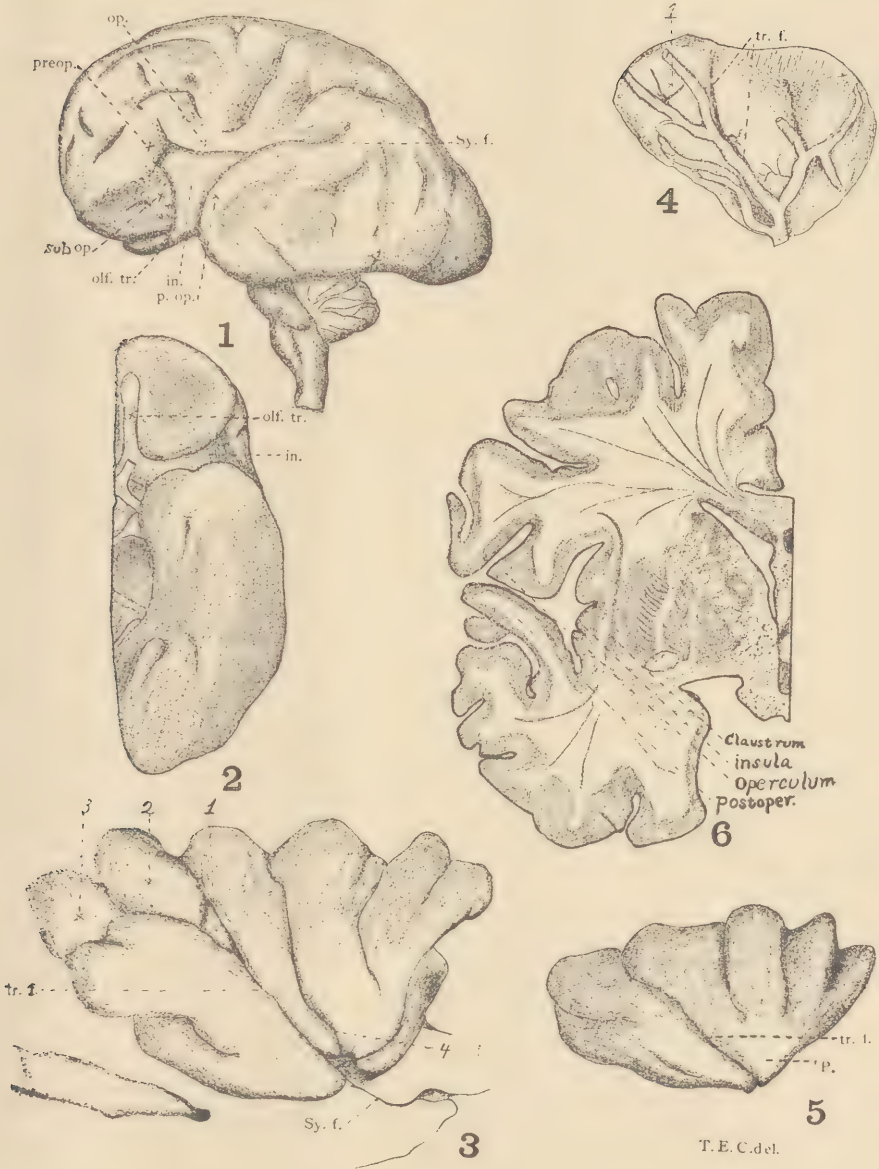
Fig. 31. Lateral aspect of the left cerebrum of a Malayan tapir (*Tapirus malayanus*), age and sex unknown, 2123; x 1. Dorsal portion of the cerebrum not shown; insula exposed by removal of overlapping parts.

Fig. 32. Lateral aspect of the left cerebrum of a sheep (*Ovis aries*), sex and age unknown, probably young; x 1. Shows the insula exposed before dissection.

Fig. 33. Dorso-lateral aspect of the right insula of a sheep (*Ovis aries*), sex unknown, probably young; x 1. Insula exposed by cutting away dorsal overlapping portions.

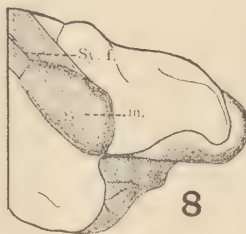
Fig. 34. See description under Plate XI.

Fig. 35. Lateral aspect of the insula of a Porpoise (*Globicephalus melas*), female, adult, 670; x 1. Insula exposed by cutting away of the operculums. *Sy. f.* designates the basisylvian fissure between the temporal and frontal lobes.





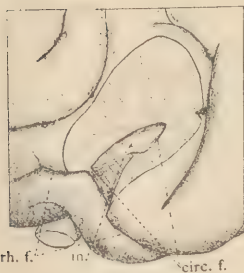
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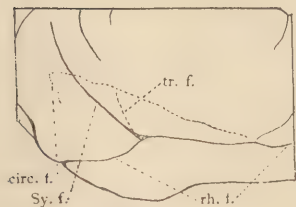
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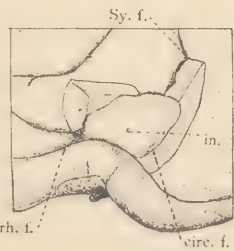
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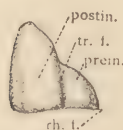
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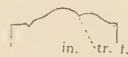
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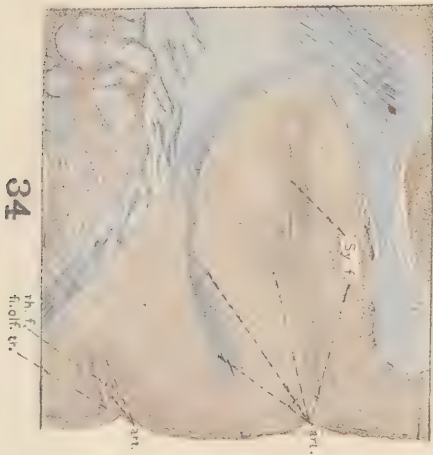
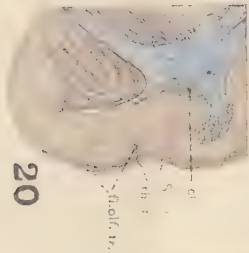
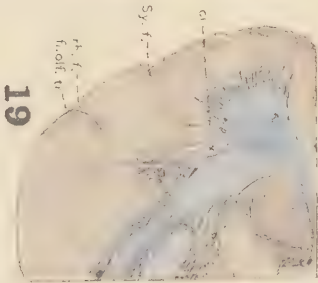
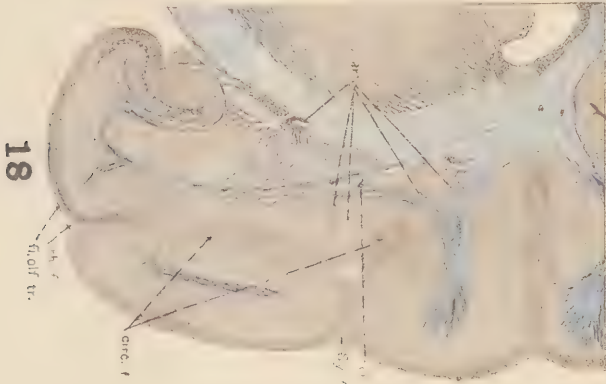
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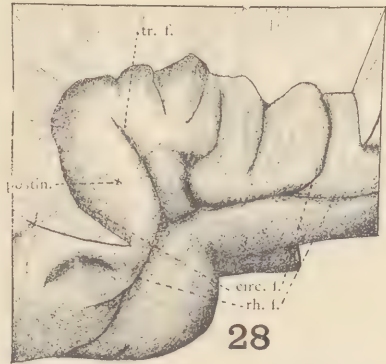
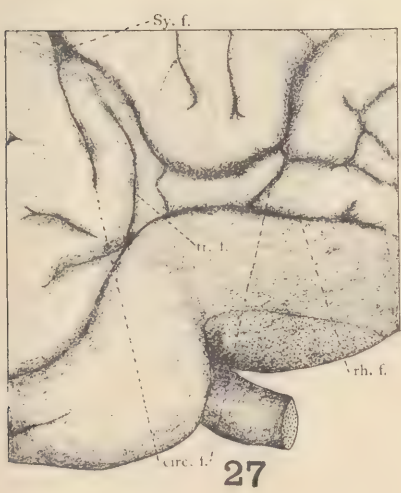
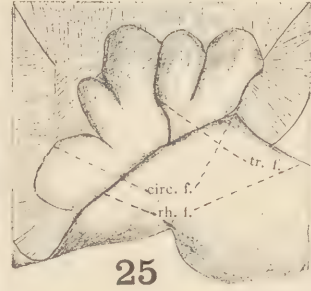
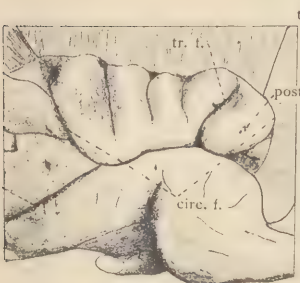
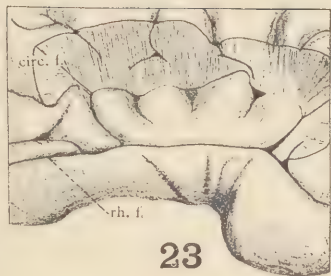
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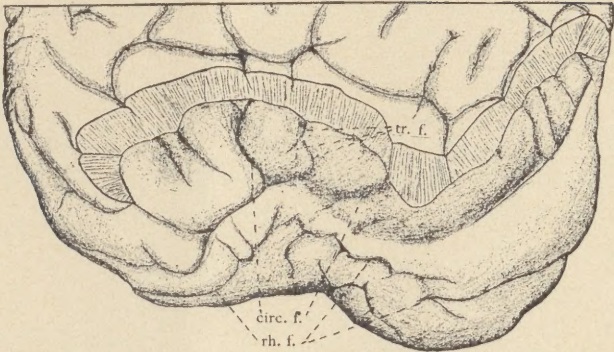


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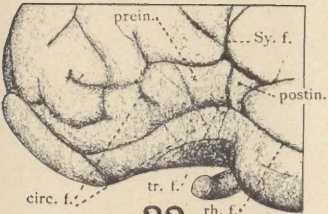


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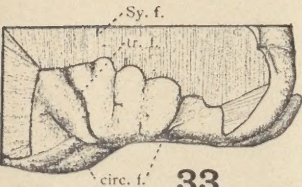




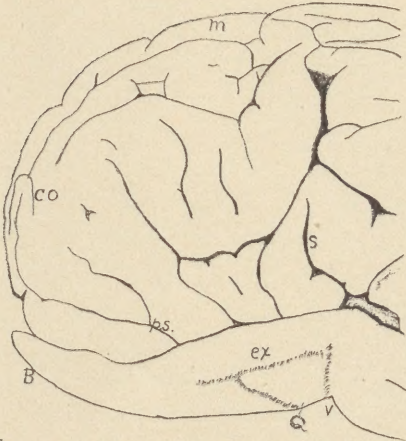
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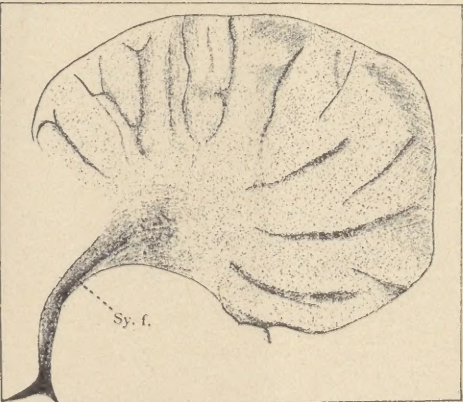
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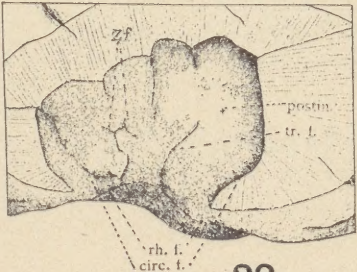
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